THE ROMANES LECTURE
1894

The
Effect of External Influen
upon Development

BY

AUGUST WEISMANN, M.D., PH.D., D.(
PROFESSOR IN THE UNIVERSITY OF FREIBURG IN BREISGAU

DELIVERED

IN THE SHELDONIAN THEATRE, MAY 2, 1894

WITH ANNOTATIONS BY THE AUTHOR

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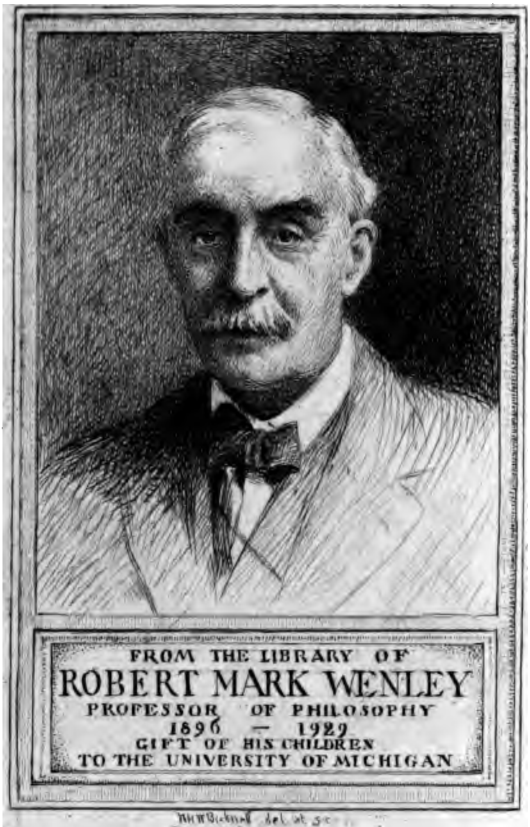
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THE ROMANES LECTURE 1894

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AUGUST WEISMANN

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PREFACE

The Romanes Lecture for 1894, as now published, is considerably longer than as originally spoken. In reading the Lecture some portions were omitted, which, although essential for the full appreciation of the argument, were not required for understanding its main drift. These passages have been restored to the text; and some notes have been added. I am indebted to Mr. Gregg Wilson for translating the Lecture into English, and to Prof. W. N. Parker for much help in the revision.

The manuscript had already gone to press when the news reached me of the sudden death of the Founder of the Lectureship. George Romanes has gone from among us. Though the state of his health for the last few years had made it improbable that a long life would be granted to him, no one thought the end was so near when, on the 2nd of May, he was present at

the delivery of this lecture and followed it with a lively interest.

His early death is a sad loss to the science for which he had still much to achieve; yet few have better used the time fate has allowed them. He worked with unwearying energy, and a long list of valuable writings bear witness to his fine gift of observation, his keen critical intelligence, and his great facility of exposition. In the very last month of his life he had set himself to solve a problem which he had originally, with prophetic insight, put forward a considerable time ago, and which he again followed out with increasing interest when biological enquiry had brought it to the front. Thus his ceaseless energy ended only with his life.

Of him it may be said—and nothing higher can be said of any distinguished man—he used to the greatest possible extent the gifts with which Nature had so abundantly supplied him.

AUGUST WEISMANN.

FREIBURG I. BR.,
May 27, 1894.

THE EFFECT OF EXTERNAL INFLUENCES UPON DEVELOPMENT

Nägeli's conception with regard to the evolution of the organic world I have always regarded as a surprising one. He supposed that it had originated in virtue of inherent internal forces, and that external influences had co-operated only secondarily and unessentially,—improving and modifying, but not determining. This acute thinker stated plainly that in his opinion the course of development would, on the whole, have resulted pretty much as it has done, even if the conditions of life had remained unchanged from the earliest times.

I do not mention this view in order to criticize it, having already done so long since: at the present day there are probably few naturalists who adhere to it. It was in a sense a last effort to save at least a remnant of the abandoned 'creation-hypothesis,' a motive force being ascribed to organisms, instead of their development being deduced from the interaction of external and internal forces—that is, from the action of the outer world upon the organism.

It is difficult to disbelieve in the potency of external influences when one sees how invariably all the vital manifestations of animals and plants are ultimately reactions to such influences, and how both animal and plant are comparable to machines so constructed that stimuli from the outer world cause them to act in the most purposeful manner for their own maintenance. How would they have become adapted in so wonderful a degree to these stimuli if they had not themselves helped in any way to bring about the result? And as every vital manifestation is a reaction to stimulus, there is hardly anything left for a developmental force to do.

Although, in my opinion, we are now quite justified in denying that evolution has taken place owing to purely internal causes, it can by no means be said that we are yet quite clear as to the way in which external influences have formed and transformed organisms. There is still a conflict between rival theories, and important points, though often apparently clear, are in reality not so.

To one such point I wish to direct your attention to-day.

It is often assumed, without much proof, that a certain variation of a living being is the direct consequence of an external influence simply because the variation in question is, in fact, in some causal connexion with a definite external influence: such an assumption is, however, founded on a totally false idea as to the interconnexion of the phenomena. In many cases this will readily be granted.

Suppose, for instance, that we assert that cold is the actual cause of the winter-sleep of marmots. It is clear that this statement is incorrect, and that not the cold, but the peculiar organization of the marmot causes the reaction of hibernation: cold cannot throw a dog or a bird into a state of slumber for the winter. We are here, therefore, concerned with a special adaptation of the organism to a stimulus—cold—which affects it in such a manner that it escapes from what would otherwise be a destructive influence. We are unable to demonstrate with the microscope the fine 'molecular' or histological variations in the nervous and other systems on which the capacity for hibernation may depend; but some such modifications must exist, and they cannot be regarded as a direct effect of the cold, but must rather be looked upon as arrangements to counteract its influence. Their origin, moreover, can only be assigned to processes of selection.

A thousand other cases are to be explained in a similar manner.

The leaves of a *Mimosa*, on being touched, bend down and close, the touch merely serving as an exciting stimulus: the actual cause of the movement is due to the peculiar constitution of the plants. The recent observations of Stahl and Haberlandt (see Note I, p. 55) have shown more clearly than ever the advantage which accrues to the plant by this sensitiveness of the delicate leaves; for by its means the plant can to some extent escape from the effects of the falling drops of a tropical rain-shower, by exposing the edges only of the leaflets to its violence.

Recent advance in our knowledge of the physiology of plants has, however, resulted in showing that much commoner phenomena of plant-life must depend upon adaptation, and are not mere products of the general constitution of the plants. I cannot help expressing my wonder and admiration at the recent achievements of botanical research in analyzing the reactions of the parts of plants to external influences with such a degree of certainty and clearness. *Gravity* determines the growth of roots vertically downwards and of stems vertically upwards, and this 'geotropic' sensitiveness is so delicate that even on the unsteady foundation of the floating shoots of *Utricularia* the flower-stalks rise perpendicularly to a height of 4–5 centimeters, and so exactly as to remain standing erect and to display their flowers—even though, with a very slight deviation, they would necessarily turn over and fall into the water.

How exceedingly important, too, are the consequences of the sensitiveness of plants to *light*;—what infinitely fine gradations in this sensibility occur in the reactions of the parts of plants, and how exactly is it adapted to their needs! A superficial observer might imagine that we are here concerned, not with adaptation, but with an original peculiarity of plants; but it is well known that the modes in which plants or the parts of plants react to light are very different, and these modifications of their general sensitiveness to light depend on differences in the fine molecular structure of their living substance. The shoots of most plants incline towards the light or are 'positively heliotropic';

while others, such as the climbing shoots of the ivy and pumpkin, turn away from it, or are 'negatively heliotropic.' As these differences are highly purposeful—inasmuch as in one case they put the plant in a position to make the utmost use of the light, and in the other enable it to climb—we must look upon the differences in structure which cause them as due to adaptation. Once more therefore we have no other explanation of their origin than that offered by selection (see Note II, p. 56).

In all these instances we have to deal with hereditary structures, that is with arrangements which always develop in the same manner under the ordinary conditions of life and growth, and which in their turn regulate the plants, so that they respond in a fitting manner to external stimuli.

Similar arrangements also exist in animals, and play an important part in their development.

Hermann Meyer seems to have been the first to call attention to the adaptiveness as regards minute structure in animal tissues, which is most strikingly exhibited in the architecture of the spongy substance of the long bones in the higher vertebrates. This substance is arranged on a similar mechanical principle to that of arched structures in general: it is composed of numerous fine bony plates so arranged as to withstand the greatest amount of tension and pressure, and to give the utmost firmness with a minimum expenditure of material. But the direction, position, and strength of these bony plates are by no means innate or determined in advance: they depend on circumstances. If

the bone is broken and heals out of the straight, the plates of the spongy tissue become rearranged so as to lie in the new direction of greatest tension and pressure: thus they can adapt themselves to changed circumstances.

Wilhelm Roux has given an explanation of the cause of these wonderfully fine adaptations by applying the principle of selection to the parts of the organism. Just as there is a struggle for survival among the individuals of a species, and the fittest are victorious, so also do even the smallest living particles contend with one another, and those that succeed best in securing food and place grow and multiply rapidly, and so displace those that are less suitably equipped. The three factors in the process of selection—variability, heredity, and struggle for existence—are all present. Processes of selection must thus take place amongst every kind of units within the organism,—not only in cells and tissues, but also in the smallest conceivable living particles, which I have called 'biophors.' Everywhere equivalent parts are contending one with another, and everywhere it is the best that prevail. We can describe this process as *intra-individual* selection, or more briefly, as *intra-selection.*

It is impossible for me to give an exhaustive account of Roux's argument here, and I must venture to assume that you are familiar with it. But there is one point I must not leave unnoticed: namely that relating to the cause which gives the advantage to one particle over others, and the consequent possibility of a struggle. This cause is to be sought in the relative power of

reaction to a definite stimulus, and in the fact that a functional stimulus strengthens an organ. Just as the contraction of a muscle strengthens it, so also is every other histological element better nourished when acted on by the specific stimulus to which it is adapted. The varied sensitiveness for specific stimuli here has a similar result to that which follows in the case of the individual possessing certain advantages which make it victorious in the struggle with other individuals. In whatever part of the organism a definite stimulus is at work, there will necessarily be an increase of those elements that are most susceptible to this stimulus and are excited to the highest degree of activity by it. Thus elements which are stimulated to growth and increase by tension and pressure, necessarily accumulate and arrange themselves in the direction of the stimulus in the parts where these forces act most strongly upon them. The arrangement of the spongy tissue of bones and of the complicated felting of the connective tissue in the dolphin's fin, as well as the marvellously suitable form and direction of blood-vessels, are thus to be explained; and we may in general say that a similar explanation can be given to the various delicate adaptations of the tissues of the higher animals, all of which have the power of adapting themselves to the present circumstances of the organism (see Note III, p. 57).

Roux, however, went further, in that he believed that these histological structures arose entirely by intra-selection, and not by individual selection at all. In this respect I believe he was wrong, though one cannot

help being struck by his question as to the origin of such minute adaptations by means of ordinary selection. Even supposing that here and there a variation of a few spongy plates happened to arise by chance, how could these give the individual any advantage in the struggle for existence, when hundreds and thousands of them are required to make the bone better adapted for its work, so as to give to the variation a selective value? In reply I should like to ask if there is no possibility of assuming that the primary constituents (*Anlagen*) of a tissue occurring in many parts of the body might be improved by natural selection acting on the germ alone. Can we suppose that the feathers of birds or the hairs of mammals have originated singly by selection? In this case it is clear that intra-selection can have taken no part in their origin.

It seems to me that Roux (see Note IV, p. 57) would not have fallen into this error if he had brought forward his ingenious conception at a later period, when the question of the inheritance of acquired qualities was more fully appreciated. In the year 1881, when Roux published the views here briefly alluded to, a few scientific men had certainly expressed some doubt as to whether an inheritance of acquired characters could actually take place; but nevertheless the idea had not been followed up, nor had it been pointed out how thoroughly our conceptions as to the causes of the transmutation of species must become changed if such an inheritance should not occur. Thus we certainly cannot reproach Roux for having accepted this supposition, and for having applied it to his own theory.

He assumed that the histological adaptations might arise by means of intra-selection alone, imagining that its results in a certain individual could be transmitted to the offspring, and thus gradually increase from one generation to another. He even emphasized this particular point, justly conceiving that such finely elaborated adaptations could not have arisen in *one* lifetime, but must rather have appeared in the course of generations; and he saw no other way in which this could be accomplished except by the transmission of acquired characters.

But there is another way out of the difficulty, and if I am not very much mistaken, Roux himself would now be inclined to regard it as the right one. It is not the particular adaptive structures themselves that are transmitted, but only the quality of the material from which intra-selection forms these structures anew in every individual life. Peculiarities of biophors and cells are transmitted, and these may become more and more favourable and adaptive in the course of generations if they are subject to natural selection. Thus in the course of generations the sensitiveness to tension and pressure has increased in certain of the primary cells of the bones, and it is this sensitiveness which now in every individual life gives opportunity for the processes of intra-selection. It is not the particular spongy plates which are transmitted, but a cell-mass, that from the germ onwards so reacts to tension and pressure that the spongy structure necessarily results. The case is quite similar to that of plants, in which geotropic sensitiveness makes the root grow down-

wards and the shoot upwards, while the branches pass obliquely outwards. The sensitiveness—the positive or negative geotropism—is inherited, and depends on the nature of the germ; but the special direction which the growing part takes is a consequence of the varying conditions of existence of the individual; it is acquired anew in every individual life, and cannot be transmitted. The great significance of intra-selection appears to me not to depend on its producing structures that are directly transmissible,—it cannot do that,—but rather consists in its causing a development of the germ-structure, acquired by the selection of individuals, which will be suitable to varying conditions. *Intra-selection effects the special adaptation of the tissues to special conditions of development in each individual.* When a tree is crowded by other trees on one side, and is thus cut off from the light, it grows less rapidly on this side, but develops all the more luxuriantly on the other: the hereditary so-called 'molecular' constitution of its shoots, which we speak of as positive heliotropism, is the cause of this. Similarly, when a fractured bone heals out of the straight, the plates of the spongy portion again become set in the line of greatest tension and pressure, the cause being the hereditary molecular sensitiveness of the connective tissue-matrix of the bone.

We may therefore say that intra-selection effects the adaptation of the individual to its chance developmental conditions,—the suiting of the hereditary primary constituents to fresh circumstances. But these primary constituents themselves could only be produced by

personal selection, and not by intra-selection. The value of the principle of intra-selection does not seem to me, however, to be diminished on this account: it still remains of the very greatest importance, for without it no higher organism could either persist or exist, or even possibly have become developed. For were this not so, the organism would be formed from the egg much in the same way as a building would be constructed every stone of which was prepared before the site or the neighbourhood in which it was to be erected had been chosen, or even the use to which it would be put had been decided upon. Such an ontogeny, predetermined in every detail, would no more produce an organism fit for life, than—as Roux has aptly put it—would a commander be victorious, who, instead of giving general instructions to his chief officers as to the placing and movements of their troops, should in advance issue detailed orders for the conduct of every one down to the lieutenants, or even to each private soldier. The influences which encounter organisms during their development are never exactly similar, and to adapt themselves to these the organisms must have a certain amount of freedom.

These influences, moreover, are by no means purely of an external kind, but are to a great extent exercised by one part of the organism on another, by cell on cell, by tissue on tissue, by organ on organ. If I am not mistaken, the phenomenon which Darwin described as *correlation*, and justly regarded as an important factor in evolution, is for the most part an effect of intra-selection, which has great influence on phylogeny

as well as upon ontogeny, even though its results are not transmitted.

Let us take the well-known instance of the gradual increase in development of the deer's antlers, in consequence of which the head, in the course of generations, has become more and more heavily loaded. The question has been asked as to how it is possible for the parts of the body which have to support and move this weight to vary simultaneously and harmoniously if there is no such thing as the transmission of the effects of use or disuse, and if the changes have resulted from processes of selection only? This is the question put by Herbert Spencer as to '*co-adaptation*,' and the answer is to be found in connexion with the process of intra-selection. It is by no means necessary that all the parts concerned—skull, muscles and ligaments of the neck, cervical vertebrae, bones of the fore-limbs, &c.—should simultaneously adapt themselves *by variation of the germ* to the increase in size of the antlers; for in each separate individual the necessary adaptation will be temporarily accomplished by intra-selection—by the struggle of parts—under the trophic influence of functional stimulus. The improvement of the parts in question, when so acquired, will certainly not be transmitted, but yet the primary variation is not lost. Thus when an advantageous increase in the size of the antlers has taken place, it does not lead to the destruction of the animal in consequence of the other parts being unable to suit themselves to it. All parts of the organism are in a certain degree variable and capable of being deter-

mined by the strength and nature of the influences that affect them; and this capacity to respond conformably to functional stimulus must be regarded as the means which make possible the maintenance of a harmonious co-adaptation of parts in the course of the phyletic metamorphosis of a species. Herbert Spencer has given it as his opinion that in the harmonious working together of parts a cogent reason is to be found for accepting the doctrine of the transmission of acquired characters: but in so doing he has overlooked the fact that there is a never-resting principle at work which is uninterruptedly concerned with the production of harmony, alike in respect of size and functional activity, among parts that co-operate: I mean the principle of intra-selection.

Naturally the degree of discord among the parts may sometimes be such that intra-selection is not able to produce harmony; for there must be definite limits to the scope of adaptation, and we well know that the exercise of a function for too long a time or too violently ceases to produce strengthening of the organ, and causes weakening instead. But as the primary variations in the phyletic metamorphosis occurred little by little, the secondary adaptations would probably as a rule be able to keep pace with them. Time would thus be gained till, in the course of generations, by constant selection of those germs the primary constituents of which are best suited to one another, the greatest possible degree of harmony may be reached, and consequently a definitive metamorphosis of the species involving all the parts of the individual may occur.

The 'reducing divisions' of the germ-plasm and the mingling of the moieties of parental germ-plasm in fertilization must be of the utmost importance in this connexion, for they secure the constant presence of an abundance of very varied combinations of primary constituents.

I should, moreover, suppose that *perfect* harmony of the primary constituents of the germ, such as would render the gradual adaptation of parts during the development of the organism unnecessary, is never in any case attained to. This seems to me as little possible as that any organ should ever become *absolutely* perfect. No adaptation is more than *relatively* perfect: this fact is involved in the principle of selection, which I believe to be unable to carry improvement further than the point at which the species becomes capable of maintaining its existence. And in like manner the harmony of the primary constituents which are contained in the germ-plasm can never become more complete than is necessary just to produce, with the help of intra-selection, an individual sufficiently capable of acting its part.

A complete harmony of the primary constituents can therefore never exist in the germ-plasm of sexually produced individuals; for this germ-plasm is always composed of two individually distinct halves. If, at any rate, those are right who agree with Darwin, Galton, de Vries, and myself in believing in a preformative arrangement of the germ-substance—that is, in a germ-substance composed of primary constituents (*Anlagen*)—it follows that in every act of fertilization

very different primary constituents of corresponding parts, derived from both father and mother, must meet in the germ.

As a rule the parts of the adult parents are so different that they could not be interchanged without the formation of monsters; and similarly the primary constituents of their germ-substance could not be united together to produce a young organism, exhibiting harmony in its various parts, if they did not all have a certain scope for variation, so as to render them capable of adaptation to one another. And though we know so little as yet of these hidden processes, we can hardly err in thinking that relations are here involved which are included in the idea of intra-selection. The struggle of parts unequal in strength—that is, unequal in susceptibility to stimulus—must be the cause which brings about the mingling of parental primary constituents, and prevents the occurrence of monsters with parts ill adapted to one another.

Intra-selection apparently also renders it possible for a harmonious organism to live and undergo development from an only moderately harmonious mass of primary constituents, such as I imagine constitute the germ-plasm. But the supposition of the whole activity of intra-selection presupposes the specific sensitiveness of the various primary constituents and of the units of smaller or larger groups of these; and this sensitiveness can naturally only have arisen through ordinary selection of individuals, owing to variation of the germ. For it is hereditary in this case just as in that of plants, the sensibility of which—(geotropic, heliotropic,

anisotropic, anisomorphic, &c.)—dominates their whole growth. All these reactions of the organism to external influences are thus to a certain extent prearranged and provided for long in advance.

I do not mean by this that the organism cannot be affected by external influences for which it is not adapted in advance. There are numerous examples known in which unusual climatic conditions have produced changes in animals and plants. European dogs sometimes lose their hair under the influence of Indian heat, and we have here a clear proof that their organism is *not* adapted for the endurance of heat. A small ruddy-gold butterfly, *Polyommatus phlaeas*, acquires a black tinge when it comes to live in warmer climates, such as that of Southern Italy. This, again, is not to be regarded as an adaptation, but must be looked upon as a direct effect of warmth. This has been shown by Merrifield's experiments (see Note V, p. 58), the results of which agree with my own observations. In this and several similar cases there is no ground for supposing that the reaction of the scales of the butterfly is, so to speak, an intentional one—or more correctly, that the determinants of the scales were so arranged in advance by natural selection that they should produce black under the influence of a high temperature.

But in other and to all appearance similar instances the relations may be of a different nature, though at a glance it may be impossible to definitely decide that this is the case. We must at any rate be careful not to regard as necessarily accidental all the variations

that appear under the influence of temperature. Many years ago I made experiments with the seasonally dimorphic butterfly *Vanessa levana-prorsa*, and was able to prove that the two forms of one and the same species, while very different in colour and pattern, owe their difference to the effects of different degrees of warmth during the pupal stage: it is at least possible to convert the summer generation into the spring form by lowering the temperature. Even at that time it appeared to me doubtful whether such a total change in colour and pattern in the summer form of *V. prorsa* could actually depend only on the chance influence of a higher temperature, and the idea of mimicry at first crossed my mind. But now, by the united labours of many excellent observers, we know that mimicry is of a much commoner and more widespread occurrence than could formerly have been supposed, and I should now consider it possible that the summer form, *V. prorsa*, might have resulted from imitation of *Limenitis sibylla*, which flies with it in clear spaces in the woods, and to which in fact it is strikingly similar. I cannot however at present give a proof in support of this supposition, and am not even able to say whether *Limenitis* is to be included among protected species. The reasons which lead me to this conclusion cannot be given here in detail, and I mention the idea only as an illustration—whether real or imaginary—of how the impression might arise that a metamorphosis was due to external influences, while the influence—in this case warmth—had only to play the part of the stimulus, the real cause being a variation

of the primary constituents of the germ produced by processes of selection,—in this instance by adaptation of the summer generation so as to render it similar to a protected species which flies about along with it (see Note VI, p. 59).

Thus it would not be inconceivable that the caterpillars of a species which produces two generations in a year should have become adapted in respect of protective colouring to two different and alternating food-plants; and in this case too, the periodic change of colour would *apparently* depend on the direct influence of the summer and autumn climate, while really due to the presence of double primary constituents in the germ, which by some external influence—perhaps warmth or perhaps the quality of the light falling on the young caterpillar—would only undergo development alternately.

It is possible that the caterpillars of the North American butterfly *Lycaena pseudargiolus* offer such an instance. W. K. Edwards in his admirable work on the Butterflies of North America says that the caterpillars of the summer and autumn broods in this species are quite differently coloured, the former being white and well protected on the white flower-buds of their food-plant, *Cimicifuga racemosa*, while the latter are yellow-green or olive-green, and live on the flower-buds of a plant (*Actinomeris squamosa*) which bears yellow flowers and blooms later in the year. Whether the last-named colouration is also to be regarded as protective unfortunately cannot be determined from the available observations, as the case would have

to be investigated specially from this point of view before it could be regarded as one of seasonal double adaptation.

Cases of seasonal protective dimorphism in many Arctic mammals and birds have, however, long been known, and only differ from the instance just mentioned in the fact that the two kinds of adaptive colouration do not concern two successive generations, but appear successively in the same individual. In these cases, also, an external stimulus—cold—seems to decide whether the summer or the winter coat is to be developed. A complicated nerve-mechanism must here exist, which, at the stimulus of a certain temperature, affects 'that part of the nervous system which presides over the nutritive and chemical changes involved in the growth of hair and the appearance of the bubbles' of gas in it. A few careful observations have been made which prove this to be true. Take, for instance, those of Captain J. Ross on a Hudson's Bay Lemming. As long as the animal was kept in the cabin, and so shielded from the low temperature, it retained its summer coat through the winter; but after being placed on deck in a cage, and exposed to a temperature of 30° below zero, it changed colour and became almost entirely white at the end of a week[1].

But while seasonal adaptive dimorphism can at

[1] This experiment is cited in detail by Poulton, from whom the above quotation is taken ('The Colours of Animals,' London, 1890, pp. 94 and 100). The whole question as to the causes of the change of the summer- and winter-coats in mammals and birds, which is here only briefly referred to, is dealt with in detail in this book.

present only be supposed to occur, another kind of dimorphism is known with certainty, in which also protective colouration is involved. In this case the nature of the colour to be developed is determined by the quality of the light radiating from the surroundings of the animal. Most of you must be familiar with the beautiful experiments of Professor Poulton on caterpillars and pupae, which demonstrate this. The caterpillars of *Amphidasis betularia* take on a colouration similar to that of the twigs on which they live from the first; and one can cause them to become 'black, brown, or bright green by the presence of similarly-coloured twigs (or paper) in their surroundings, although fed on the same food[1].' In like manner the pupae of *Vanessa urticae* become dark blackish-brown when they undergo transformation on a dark ground; but assume a light colour or even a strong golden sheen when they have settled on a light ground. In these cases, again, it cannot be supposed that the primary constituents for polymorphism have possibly arisen directly owing to the light; they must rather have been produced as an adaptation by processes of selection. But each of the possible colours of the skin originating in this way is specially sensitive to certain kinds of light and is roused to activity by these alone.

This instance leads us to those in which the same individual is able to change colour in a short time—

[1] Cf. E. B. Poulton, 'Further experiments upon the colour-relation between certain lepidopterous larvae, pupae, cocoons, and imagines and their surroundings,' Trans. Ent. Soc., London, 1892, p. 293.

in fact, almost momentarily—as is the case in many fishes, amphibians, reptiles and cephalopods. The light that calls forth the colour does not here act directly, or at any rate principally, on the elements of the skin that produce the colour; but a complicated nervous apparatus exists connecting these and the part that is first stimulated by the light, viz. the nerve-endings in the skin or in the eye. If in the latter case the optic lobes of the brain are artificially destroyed, the capacity for changing colour ceases: it therefore depends on a reflex mechanism, the origin of which, again, cannot be attributed to any cause acting directly, but can only be referred to processes of selection.

In these and similar instances, the dimorphism is not consequent on double sets of primary constituents of which only one or the other can attain to development: it depends on the different susceptibilities of the histological elements which in exquisite combination make intra-syle up the skin.

Many facts indicate that the *differentiation of sex* can also within certain limits be regarded from a similar point of view. The primary constituents for the characters of both sexes are included in the same egg, and in many instances it appears that a stimulus decides as to which group of them shall undergo development—whether the male or the female. Unfortunately in only very few cases can we as yet determine the stimulus with certainty, but we are at any rate certain that it is not the same in every instance. Yung's well-known experiments indicate, in the case of tadpoles, that the sex is partly determined by the nature and

amount of their food; and similar results have been obtained by several observers with regard to certain caterpillars, in which, as in tadpoles, the males appear in greater numbers when nourishment is scarce. Experiments made by Maupas, on the other hand, show that in *Hydatina senta*, one of the fresh-water rotifers, the determination is effected by the temperature; and this instance is specially interesting, as the sex of the offspring is decided even before their primary constituents are formed in the germ (see Note VII, p. 60).

Siebold and Leuckart have shown that in bees and wasps the eggs which are fertilized develop into females, while those that are not fertilized give rise to males. And though we are still completely in the dark as to how this occurs, its utility at any rate is manifest, for the queen is thus enabled to produce male or female offspring at will or according to necessity. To this extent we can understand why the sex has here been made to depend on an external impulse; and probably no one would in this case conclude that the stimulus is the efficient cause of the male or female character of the embryo: no one regards the warmth necessary for the development of a pigeon's egg as the cause of its giving rise to a pigeon and not to a duck (see Note VIII, p. 60).

In other instances, however, this is less apparent, and the stimulus is readily mistaken for the *causa efficiens* of the development. Permit me to go somewhat more into detail with regard to one such case which seems to me of peculiar interest; and which, although generally known, has never yet been

thoroughly explained. I refer to *the neuters or workers of state-forming insects—bees, ants and termites.* As is well known, these workers do not originate from special eggs, but it has been demonstrated in bees and termites, and shown to be very probable in the case of ants, that there is only *one* kind of egg, from which queens and workers as well as males arise. When female larvae are supplied with a very rich and nourishing diet, they give rise to queens; but workers are developed if the larvae receive scantier and less nourishing food. The differences between these two castes are manifold; but at present I wish to call your attention to one characteristic only, namely, *the sterility of the workers*—their relative or, in certain cases, absolute barrenness.

Let us inquire, in the first place, how this sterility has arisen. Many would possibly suppose that it is a direct consequence of the poorer nutrition of the larva. This view has frequently been maintained[1], and has been repeated by Herbert Spencer quite recently; but I cannot look upon it as a correct one in the sense implied. It is certainly true that bees have it in their power to cause a larva to become a queen or a worker according to the manner in which they feed it: it is equally true of all animals that they reproduce only feebly or not at all when badly and insufficiently nourished: and yet the poor feeding is not the *causa efficiens* of sterility among bees,

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[1] For example by William Marshall in his delightful little work *Leben u. Treiben der Ameisen.* Leipzig, 1889.

but is merely the stimulus which ***not only results in the formation of rudimentary ovaries, but at the same time calls forth all the other distinctive characters of the workers.*** It appears to me to be doubly incorrect to look upon the poor nourishment as the actual cause; for such a view not only confuses the stimulus with the real cause, but also fails to distinguish between an organ that becomes rudimentary and one that is simply imperfectly developed. Moreover the fact is overlooked that the ovaries of the workers are actually rudimentary organs: a great proportion of their really essential parts have disappeared, while only a small remnant is retained. The ovary of the queen-bee consists of from 180 to 200 egg-tubes, and numerous eggs may become mature in one of these. The queen is accordingly able in the course of her life to produce an immense number of eggs,—more than a hundred thousand. The ovary of the worker on the other hand contains from two to six egg-tubes only, and no matter how rich the food may be, no more can be formed in the imaginal state. The workers certainly produce eggs occasionally, when they have received exceptionally rich nourishment in the imago-stage; but even then their fertility is never great, for only a few eggs can find room to ripen at a time in the small number of ovarian-tubes present. And this is only exceptional, for the workers ordinarily only take just enough food to serve for the sustenance of the body, and not sufficient to allow the small egg-germs in their ovarian-tubes to become ripe.

It is now possible to show by experiment that poor

nourishment does not induce any degeneration of the ovaries of insects.

In many respects flies (*Diptera*) resemble bees from a biological point of view: they develop from footless maggots, which live in the midst of suitable nourishment and absorb food almost without interruption. They grow rapidly, and after a short rest in the pupal stage develop into the perfect insect and reproduce abundantly soon afterwards. I reared large numbers of the eggs of a female blow-fly (*Musca vomitoria*) (see Note IX, p. 61), after separating them into two lots, one of which was uninterruptedly supplied with rich food, while the other was most sparingly fed. In the latter case the larvae were from time to time removed from the flesh into which they had bored and left for a number of hours without food. These larvae grew slowly, and all remained more or less noticeably small. But in point of time their development was not delayed: they underwent metamorphosis simultaneously with the normally fed larvae, only a few of them being one day later. In both cases the larval period lasted from nine to ten days and the pupal stage for from twenty-eight to twenty-nine days. Almost simultaneously all of the several hundreds of flies escaped from the pupa; and from that stage onwards they were kept in large airy cages exposed to the sun, and were well supplied with food (see Note X, p. 62).

Now if the reproductive organs had remained rudimentary in consequence of the poor nourishment, this would necessarily have become apparent by the ill-fed

flies not reproducing, or doing so only feebly. But this was not the case: though they were all smaller than ordinary flies—many of them indeed being strikingly small, having doubtless absorbed less food than the normally fed larvae,—yet on the 6th of June, the same day on which the flies derived from the latter began laying eggs, they too laid abundantly for the first time. And the matter did not stop here, for the process was often repeated subsequently. In order to be sure, however, that even the smallest of them,—that is, those which had been most affected by the bad feeding—were reproducing, I isolated five of the smallest flies. After seven days they had produced two large packets of eggs; and this process was repeated four times within the next fortnight.

There could therefore be no doubt that, in spite of the scanty supplies of food during larval life, the organs of reproduction, or at any rate their essential part—the ovaries, were normally constituted; so that with good nutrition during the imago-stage these flies reproduced in a perfectly normal manner.

I was however able to prove that the external re productive parts were also normally developed. number of females were isolated in small cages imm diately after their escape from the pupa and abundant fed. These too in course of time laid eggs, not a sing one of which developed into a larva. It therefo follows that the eggs of *Musca vomitoria* lack t capacity of developing parthenogenetically; and hen *all the eggs of the ill-fed flies were fertilized.* T however would only have been possible if the ent

male reproductive apparatus was normally developed. My experiment proves this fact more clearly than could have been done by anatomical investigation; and evidence is thus afforded that no part of the reproductive organs was degenerated in any degree by limiting the food during the larval period.

By comparing the result of this experiment with the known facts as to bees, the difference in the behaviour of the two organisms is made clear. In the case of bees a distinct degeneration of the ovaries and various accessory organs of reproduction takes place in consequence of poor nourishment; while in flies the whole reproductive apparatus is formed quite as perfectly when the nourishment of the larva is deficient as when it is ample. There is even no delay in the maturing of the eggs—as is shown by the fact that the first batch was laid at exactly the same time as in the case of the flies arising from normally fed larvae.

It might, however, be said that flies and bees are very different organisms, and therefore react differently to external influences. This is quite true, and is exactly what I wish to be acknowledged. My experiments with the flies were merely meant to show that all insects, even though they may resemble bees in some respects, do not react in a similar way to the bee to meagreness of nutrition, and that accordingly *this mode of reaction is a characteristic of bees:*—it is a new acquisition, and was not possessed by the ancestors of these insects.

But nevertheless I cannot quite agree with the view of Eméry, a great authority on ants, who has recently

given it as his opinion that the degeneration of th ovaries of the workers is simply due to an increase sensitiveness of the 'germ-plasm' to poor nourishment and has explained the whole phenomenon of th formation of neuters among insects as consequent c such an altered mode of reaction in the germ-plasr If it is thereby meant that the ovary is more easi affected by slight nutrition than are the ovaries other insects, the supposition is hardly correct. fails to explain the facts; for the ovary of the worke is not only in an undeveloped condition, *but is actua rudimentary: the majority of the typical parts are wantin* Even if it be assumed that the number of ovari egg-tubes has increased in the queen since the cas of workers arose, there can nevertheless be no dou that at the same time it has diminished greatly in t case of the workers. This follows from the discoveri of Adlerz as regards ants, from which it appears th the degree of diminution in the number of egg-tub is different in different species; the number vari from twelve to one, and in the case of *Tetramoriu caespitum* they are even totally absent. But the ru mentary condition of the reproductive organs becom even more apparent when we consider that both t bursa copulatrix and the receptaculum seminis ha degenerated in the bee and ant workers; and we ha every reason for believing that typical parts cou never disappear owing to poor nourishment, no matt how poor it may have been—an egg-tube would 1 more disappear from this cause than would a leg a wing. How often have caterpillars been rear

en masse on starvation diet, either designedly or from carelessness, and yet none of them has ever given rise to a butterfly destitute of wings or to one with only four legs instead of six. Such butterflies are always very small but in other respects perfect, just as in the case of the ill-fed flies. *The disappearance of a typical organ is not an ontogenetic but a phylogenetic process; it never in any case depends on mere influences of nutrition such as affect the development of each individual, but is always due to variations of the primary constituents of the germ, which to all appearance can only come about in the course of numerous generations.*

The view that a mere increase of sensitiveness to poor nourishment is the cause of a worker's ovary consisting of few or no egg-tubes is therefore not satisfactory. We must rather suppose that the primary constituents of two distinct reproductive systems—e.g. those of the queen and worker—are contained in the germ-plasm of the egg.

But even as regards the maturation of such egg-germs as are present in the worker's ovary, we can hardly ascribe to the social insects a heightened sensitiveness to poverty of food. We do, however, find this sensitiveness developed in a high degree in many animals. Let me refer for instance to the observations I made many years ago on the disintegration of half-ripe eggs in the ovary of the Daphnidae as soon as the animals lacked a sufficiency of food[1] (see Note XI,

[1] Cf. Weismann, A., 'Beiträge zur Naturgeschichte der Daphnoiden,' Abhandlung VII: 'Die Entstehung der cyclischen Fort-

p. 62). The degree in which the maturation of t eggs of insects depends on their food is also sho by my experiments with flies, which when poorly f after reaching the imago-state produced no eggs at the ovaries remaining in the unripe condition in whi they are always found in the young imago, even wh there has been abundant food for the larva.

The facts, therefore, support neither the idea tl the degeneration of the ovary of the workers is direct consequence of poverty of nutrition, nor t view that an increased sensitiveness of the ovary the influence of nourishment is here concerned. I they do show *that poor nourishment acts as the stimu for the latent primary constituents for the workers in germ-plasm;—not only for those of the ovary, but also those of all characters by which the worker is distinguis from the queen.*

It might at first perhaps appear peculiar that and the same egg should contain double primary c stituents of numerous parts of the body; but we n not be surprised at this if we reflect that double prim constituents of many parts of the body—namely th for the male and female—must certainly be contai in the eggs of almost all animals. In a few cases th constituents are even distributed to two different ki of eggs which differ in size: take the case, for instar of rotifers and of the *Phylloxera*, in which it is c sequently beyond doubt that each sex has its c

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pflanzung bei der Daphnoiden,' Leipzig, 1876–79, or *Zeitschr wiss. Zool.* xxvii–xxxiii.

primary constituents. And if this be so in these instances we are not, it appears to me, justified in doubting that the eggs of sexually dimorphic animals in general contain double primary constituents, though these are not distributed in two distinct kinds of eggs, but are contained in the same germ-plasm. From this latter condition we pass readily to the relations that exist among the social insects, the germ of which must contain at least three sorts of primary constituents of the body, inasmuch as those of the female occur in two forms.

Let us now inquire how it is possible for the degeneration of the primary constituents of the ovary to come about. It is clear that this could not be a consequence of disuse, as infertility ceases to be transmitted in proportion as it increases. It therefore seems to me that the relative disappearance of egg-tubes in the workers of bees and ants furnishes a convincing proof that it is a mistake to regard the degeneration of any organ as a direct consequence of disuse. In the case we have been considering the very organs on which transmission depends have degenerated, and accordingly the degeneration could not be transmitted at all. The degeneration of the ovary has nevertheless proceeded on its slow phyletic course, step by step, and has caused one egg-tube after another to disappear; just as organs that are no longer used—such as the supernumerary toes of the ancestral horse—have to all appearance degenerated through the direct effects of disuse, their reduction being transmitted to subsequent generations. But in the case we were here dealing

with there are no subsequent generations! These facts cannot be too strongly insisted on, and should be carefully considered by those geologists who lay so much stress on appearances, and assume that a transmission of acquired characters is a demonstrable process, because in many or even in most cases *it looks just as if* the disappearance were a direct consequence of disuse:—appearances are often deceitful and therefore cannot be accepted in place of facts. We might as well maintain that the sun goes round the earth: better proofs to the contrary could not, I believe, be adduced in this case than are brought forward with regard to the facts just stated in connexion with the transmission of acquired characters.

We can therefore in this case only ascribe the degeneration of the reproductive organs to processes of selection: and there can be no objection to this view, for the degeneration is an advantageous arrangement, by means of which the workers were fitted to give their whole strength to work. The advantage to the colony of possessing a worker-caste has been so often shown that I need not here go into details.

A further question now arises as to how it is conceivable that two or even three kinds of primary constituents of the organs in question should be contained in one germ, and how they could have become developed. This seems to me not to present much difficulty on the principles of my theory of heredity. I suppose that the germ-plasm includes a considerable number of secondary units, each of which contains within itself all the primary constituents that

are necessary for the development of an individual: these secondary units I have spoken of as 'ids.' Starting with this assumption, there is no difficulty in conceiving that the germ-plasm of bees at the present day is composed of *different* kinds of ids, some of which contain the primary constituents of workers, some those of queens, and others those of males; and there is no reason why the worker-ids of ants should not be supposed to be of two kinds—those of workers in the strict sense of the word, and those of soldiers (see Note XII, p. 63). The 'male' ids—if I may be allowed the expression—become active in the absence of fertilization, the 'female' ids on the occurrence of fertilization, and the kind of food supplies the stimulus for the worker-ids or queen-ids. Slow processes of selection have gradually changed the 'female' ids in two directions, and finally led to the establishment of two perfectly distinct forms of females. That the process has not been sudden, but has been brought about step by step, is apparent; for even at the present day a number of stages in these metamorphoses are still to be found among the workers of the different species of ants. Moreover, sporadic transition-forms between workers and females also occur, and show varied combinations of characteristics, just as in the case of hermaphrodites that occur abnormally from time to time and exhibit extraordinary and often perfectly methodless mingling of sexual distinctions; in bees especially, wonderful combinations of the characters of both sexes have been observed.

The facts that are furnished by the gradual meta-

morphosis of the females into workers among state-forming insects give an important support to the view that the germ-plasm is actually composed of ids, and these again of primary constituents of the different independently varying parts of the body—that is of 'determinants.' It is necessary to suppose that at first only small groups of determinants varied: in the case of ants possibly those of the reproductive organs and wings, and at the same time, many of those of the brain. New determinants arose as the old ones disappeared; and as thus more and more numerous and comprehensive groups of determinants gradually underwent increased modification, a 'worker-id' finally arose. In like manner other 'female' ids were converted into 'queen-ids'; and among the ants possessing soldiers, part of the 'worker-ids' became differentiated to form 'soldier-ids.'

I cannot help thinking that the otherwise unexplained phenomena of polymorphism become clear and comprehensible,—both as actual phenomena and in their phyletic development,—if we accept the view that the germ-plasm is composed of ids—a view founded on facts of a very different kind. And it is not necessary to make any new assumptions special to this instance, for everything takes place exactly as I have supposed to be the case in all processes of transmutation. I concluded from the phenomena of heredity that at the beginning of a metamorphosis there is in all cases a variation of the determinants of those parts which have to adapt themselves to new demands of the conditions of life. But even these primary variations do not necessarily depend

on a metamorphosis of the homologous determinants of all the ids, but only of a small majority of them, which would just be sufficient to cause the development of the altered character. The number of ids thus modified increases gradually by the aid of the processes of amphimixis and reducing division; and simultaneously a change occurs in the determinants of other co-operating parts of the body, until finally most or all of them are modified in some respect—sometimes in a lesser, sometimes in a greater degree. Thus the ids in question take on an entirely new nature.

This process is the same as that conceived to occur in the formation of the workers of ants and bees—with the one difference that among these there could never be a conversion of all or even of most of the ids into 'worker-ids,' but only a definite percentage of them; for the fertile females continued to be necessary for the species, and so had to be represented by a number of ids in the germ-plasm. But in the ordinary metamorphosis of a species some of the ids, if my theory is correct, will always be retained for a long time unchanged or but little changed: this we may conclude to be the case from the phenomena of reversion. Such unaltered ids, having ceased to be important for the species, may gradually disappear by means of the reducing divisions, till at last only isolated groups of old determinants are retained in a few of the ids. But in the case of the social insects a relationship has become established between old and new ids; and this we can only ascribe to processes of selection.

If in the germ-plasm of the bee there were only one

primary constituent, possessing the power of developing into a queen under the influence of rich food and into a worker when poorly nourished, how could we explain the fact that in the latter case not only does degeneration of individual parts occur, but also a different and stronger development of other parts? It seems to me that on the grounds of the phenomena observable in the social insects alone, we have no choice but to accept the theory of ids; for only by its means does it become intelligible how totally opposite characters can be brought forth by the stimulus of poverty of food—degeneration of the ovaries, the receptaculum, and the wings, and frequently a reduction of the entire bulk of the body on the one hand; and on the other, increase and higher differentiation of individual parts, such as the brain in worker-ants and the head and the jaws in the soldiers, together with many correlated instincts. None of these variations,—not even the frequently striking small size of the workers,—originates owing to the direct action of poor food. Should we attempt to make dwarfs of any insect by starvation during the course of development, we should at most get a reduction to about half the normal size: this was occasionally the case with the butterflies and flies referred to above.

But the workers of some ants (*Atta fervens*) are ten times smaller than the fertile females; and even if a small proportion of this difference is to be ascribed to a phyletic enlargement in the females, a considerable part must without doubt be credited to a diminution in the workers. Eméry is therefore so far right in his

opinion that the origin of such dwarf workers must depend on a special peculiarity of the germ-plasm; for the defectively fed larvae were not starved to death, but underwent metamorphosis, merely remaining small. This special peculiarity of the germ-plasm, however, does not consist in an increased sensibility, and can only be the result of a complete metamorphosis of the whole germ-plasm, which in the case of the worker-ids has in fact become altered just as was necessary for the production of a body of small dimensions. For we cannot seriously suppose that these larvae are really insufficiently nourished and kept small by hunger (see Note XIII, p. 65). They get exactly as much nourishment as they need for the development of the worker-type, and as their instinct demands from the time when they have become worker-larvae owing to the poorer food (see Note XIV, p. 66). The primary constituents concerned with instinct in the worker-ids are modified, just as are those of the queen-ids. Concurrently with the visible alterations in bodily form, invisible variations have also occurred, as we may conclude from the fact that there has been variation in the instincts. But we know that the 'art' of rearing from the larva either a worker or a queen by means of a definite mode of feeding is an instinct which can only have been formed along with the development of the worker-type; moreover, the instinct of more moderate food-requirements will likewise have developed at the same time in the larva of the worker. For the worker-larva is a distinct individual with its own peculiar tendencies (*Anlagen*) and instincts, just as

much as is the full-grown worker. Bee-larvae all receive similar food for three days only, and thus long they are undifferentiated, and may become either workers or queens; but they are then fed differently, and the decision is then given as to which ids in the ontogeny shall become dominant. It would be just the same if even older worker-larvae could be converted into queens by the supply of the royal food; for the ids with the primary constituents of the queen do not disappear, but are passed from cell to cell with the other ids through the whole ontogeny; and so long as they are so constituted as to become active on receiving a certain kind and quantity of food, they might be capable of development even later, so long as the parts of the fully developed insect have not begun to develop. In the case of bees it is not so: at least bee-cultivators assert that very young larvae of from one to four days old must be selected from among the workers in order to breed up an artificial queen. But according to Grassi, the larvae of termites may also, at the will of the workers that feed them, be converted into fertile females by being supplied with more abundant nourishment, consisting of a nutritive secretion from the salivary glands of their attendants (cf. Note XV, p. 67).

It is certainly very remarkable that this adaptation of the larval organism to the determining stimulus of a specific mode of nourishment should be so perfectly similar in two such different groups of insects as the bees and termites: for there can of course be no doubt that it has arisen independently in each group. But

does not seem to me surprising that natural selection as in both these cases coupled the development of ie caste primary constituents with stimuli dependent n nutrition. This convergence seems to be as in-elligible as the independent development of similarly onstructed eyes in very different groups of animals. *What other influence could have acted as the stimulus, nd at the same time been under the control of, and ependent on, the will of the animals?*

It might be supposed that different degrees of emperature would have served this purpose equally well; but it would have been difficult to make such a stimulus effective.

Ants do at times carry their pupae into the sun; and it would doubtless have been possible for natural selection to connect the development of the primary constituents of the workers with stimuli produced by temperature, just as in the adaptive seasonal dimorphism of butterflies the different garbs of the members of the species might have been made sensitive to definite temperatures—provided it were possible for natural selection to couple the development of all the characters of the workers with the stimulus of temperature. But how would the necessary temperature have then been secured for the larvae, seeing that the animals have no control over the sunshine, and can still less command an ice-cellar?

It is however not difficult to understand how differences in nutrition came to be a determining stimulus, for the feeding of the larvae was in vogue among the solitary Hymenoptera and such as lived in small

companies long before the formation of insect-states. It was therefore possible for natural selection to step in and favour a definite mode of feeding, and at the same time to give those daughter-larvae an advantage in which some of the ids had varied in the direction of producing workers. We cannot yet however follow out the details of this process; and it would at present be premature to inquire how the poorer nourishment ever began to bring the worker-ids in particular into activity. This cannot be understood at present any more than can the peculiarity in the tissues of roots which causes them to grow downwards under the influence of gravity and not upwards, as the stems do. We must for the present content ourselves with the belief in the possibility of such a mode of reaction being provided for by processes of selection, as we know no other origin for purposeful modifications.

Thus in the whole history of metamorphosis everything apparently brings us back to selection. I have frequently been charged with exaggerating the sphere of activity of natural selection and with putting the direct effects of external influences in the background. But I hope to have shown to-day in one instance that there is sometimes a tendency to go to the other extreme, and to make external influences responsible for a metamorphosis in which they can have had no part. In the case in point, selection must be responsible for all that has become altered in the workers,—for the stunting of the ovaries, the variation in the nutritive requirements during the life of both larva

and imago, the origin of the art of rearing workers or queens at will, and for all the bodily improvements and degenerations which have taken place.

The effects produced by natural selection in the formation of insect-states are certainly wonderful and manifold; and we are quite justified in asking whether such intensive processes of selection are specially possible in the case of the state-forming insects. Several years ago Wolff[1] gave expression to the view that selection was out of the question in this case, for 'the individuals struggling for existence and those offering varieties for selection' are not the same,—the first being represented by the hive, the second by the single persons which compose it. It is true that variations of single individuals of the many thousands in a hive would be quite ineffective in the struggle for existence in which the hive as a whole has to take part. But Wolff has overlooked the fact that the hive as a whole, if not an absolute unit, varies like one, inasmuch as all its members are the offspring of one or at most of a few mothers. The fact that there is only one queen in the hive considerably simplifies and facilitates the processes of selection, all the partners of the society being sons and daughters of the same father and mother. According to Grassi's researches this is also true as regards some of the termites at the present day: in the case of *Calotermes flavicollis* there is only one true queen; and though

[1] G. Wolff, 'Beiträge zur Kritik der Darwinschen Lehre,' *Biolog. Centralblatt*, Sept. 15, 1890.

a single queen appears to be regularly wanting and to be replaced by so-called 'substitution females' in *Termes lucifugus*, this condition is secondary, and has only arisen from the other long after the differentiation of castes had taken place. To this day true queens of *Termes lucifugus* appear, but found no state, for they perish in the nuptial flight.

But I have lingered too long on the state-forming insects, and must now return to the point in connexion with which I first referred to them. I wished to show that when it is important to regulate different possibilities of development, nature makes use of external influences as stimuli. But it is not always an external stimulus that originates a change of form;—it may be an internal one. Thus in the case of several animals which exhibit alternation of generations there appear to be internal arrangements for the determination of the sequence of the various forms: I was at least unable to prove experimentally as regards the Daphnidae that temperature and the drying up of the water in which they lived caused these animals to reproduce sexually. The various species of these water-fleas are so organized that each produces a tolerably definite number of generations of females, and then only are males born. The number of these generations, moreover, is definitely regulated in the various species, so as to be most conducive to their maintenance. In those that live in large lakes the males only appear at the end of the summer, while in such as inhabit small pools, and are exposed to the danger of desiccation, early production of winter-eggs is necessary; and these, as

well as the males that are needed to fertilize them, appear as early as in the second generation.

Among related Crustacea, however, we find dimorphism of the species linked to external stimuli. Most zoologists will remember the interesting experiments and observations made twenty years ago by Schmankewitsch on *Artemia mülhausenii*, which is found in salt-water pools on the Crimean coast[1]. When the specific gravity of the water in which these animals live is gradually raised, the common species, *Artemia salina*, goes through changes which cause it to appear as *A. mülhausenii*; and it is said that when the specific gravity is gradually lowered to a considerable degree, the species varies in an opposite direction and is converted into the form formerly described as *Branchipus schäfferi*. The changes which occur are at least partly of such a nature as to be advantageous in view of the different degrees of saltness of the water:—thus an increase takes place in the size of the gills in water of higher specific gravity in correspondence with the less abundant supply of oxygen. From this I should infer that the specific gravity is not the direct cause of the change, but is only the stimulus which induces the modification of primary constituents which have originated by selection. There would thus be in this case, as in that of bees and ants, a double or possibly even a multiple adaptation of the body to varying specific gravity, and this would be consequent on a slow

[1] *Cf.* Schmankewitsch, 'Ueber das Verhältniss der *Artemia salina* zur *Artemia mülhausenii* und das Genus *Branchipus schäfferi*.' *Zeitsch. f. wiss. Zool.* Bd. xxv. 1875.

periodic variation of the latter:—certain determinants of one id would have adapted themselves to a high specific gravity; those in a second id to a lower specific gravity; and in a third, perhaps, to an intermediate condition. Along with this polymorphism a special sensitiveness of the primary constituents to varying degrees of saltness of the water would moreover have arisen, so that the right primary constituents would always be stimulated to development by the specific gravity itself.

Whether this is the right explanation, or whether and to what extent the direct influence of specific gravity co-operates through the action of intra-selection, cannot be deduced from the experiments that have so far been made; and I have only introduced this instance to point out that the way in which it is usually represented in order to illustrate the direct effects of external influences is by no means conclusive. It is quite conceivable that the saltness of the water in this case acts merely as a stimulus.

I cannot by any means claim to have exhausted my subject, and have only wished to give a few illustrations of how I imagine external influences to be made use of by nature for exciting the development of definite primary constituents of the germ. The subject is at present too new to permit of any enumeration of the influences on organisms which have been made use of as stimuli of double primary constituents; but we must *a priori* regard all kinds of influences as capable of being employed to regulate a potential development in certain circumstances. We see how

finely graduated and regulated the sensitiveness of parts may be in the case of the gradual differentiation of the body in plants and animals according to the principle of division of labour; for sensitiveness has gone hand in hand with morphological differentiation, gradually becoming more finely graduated and increased. And how wonderfully fine it can become we see by reference to the various special activities of the elements of our own body, as well as to the numerous processes of all kinds which occur both in plants and animals. For example, we know that as a rule self-fertilization is avoided among Phanerogams, that numerous complicated arrangements exist in the flowers to prevent its occurrence, and that even the very existence of many flowers depends on the fact that cross-fertilization by the agency of insects is an advantage. This presupposes that self-fertilization is always possible, and that it would always be less advantageous in these cases. But neither of these suppositions is universally true:—all degrees of sensitiveness to self-pollination exist. Many orchids which are in every respect adapted for cross-fertilization by insects, have proved to be fully fertile with their own pollen; others, on the other hand, like *Corydalis cava*, which could very easily effect self-pollination, are quite unfruitful with their own pollen: in contrast to these, again, we have cleistogamic flowers, which never open, and consequently are designed for self-fertilization only. Most striking of all, however, is the varying sensitiveness for minute differences of stimulus in the case of dimorphic and trimorphic flowers, which are so

adjusted that self-fertilization never occurs, and only the pollen from another flower of different form can successfully effect fertilization. Here, again, we seem to have an insight into the means by which this adaptation has been brought about: the pollen-grains are of different diameters, and the length of the pollen-tubes to which they give rise corresponds to that of the style of another form of flower. In most other cases we are as yet unable to observe the mechanism of sensitiveness, which is usually of a much finer kind. But a mechanism it must always be, and it can only have originated on the one principle with which we are acquainted in connexion with the origin of adaptations,—viz. by selection, based on individual variation.

Many more facts could be brought forward to illustrate the subject of the present lecture, but I fear that the numerous details I have been obliged to give may have already exhausted your patience, and lessened your interest in the general conclusions to which they lead. I will therefore conclude with a brief summary of my remarks.

It has long been recognized that external influences serve to stimulate the functions of the body, and I have attempted to show that in a great number of cases they also act in another and less apparent manner. *They are used*—so to speak—*by nature to regulate in a purposeful manner the appearance of the various forms which members of a species may take.* The germ must thus contain all the primary constituents (*Anlagen*) of these different forms; and a stimulus—produced by the kind of food, by light, by warmth, or by some other

external influence—serves sooner or later to start the development of one kind or of another, as well as to decide which kind it shall be. Various degrees of difference may exist amongst these forms; they may refer merely to the colouration and marking—as in cases of the adaptive seasonal dimorphism which I have attempted to show probably occurs in caterpillars and butterflies,—or they may be so considerable as those which exist between the castes of state-forming insects.

External influences are in none of these cases the actual cause of the differences; they merely play the part of the stimulus that decides which of the primary constituents shall undergo development. The actual cause of these individual dissimilarities is in all cases to be sought in the preformed modifications occurring amongst the primary constituents of the organism itself; and such modifications, as they are always purposeful, can only have originated by selection. Even when to all appearance external influences have had a *direct* action in causing purposeful modification, a more careful examination of the case in point will always show that in reality they have only served to incite into activity some preformed adaptation. This is shown in a specially conclusive manner by the consideration of sterility in the workers of bees and ants. The sterility is not due to poor nourishment, but to the presence in the egg, owing to selection, of the primary constituents of a *rudimentary* ovary as well as those of a *perfect* one, the former undergoing development when the young larva is less richly nourished. Poorer food serves as the impulse which starts their development.

This case is of additional interest as it may serve to convince those Naturalists who are still inclined to maintain that acquired characters are inherited and to support the Lamarckian principle of development, that their view cannot be the right one. It has not proved tenable in a single instance—not even in the particular case on which so much stress has been laid by one of the recent advocates of this doctrine.

The facts here brought forward, as well as the interpretation of them at which I have arrived, confirm me more strongly than ever in the belief that selection is the all-sufficient principle on which the development of the organic world has been guided on its course.

NOTES.

NOTE I (p. 9).

THE movements of the leaves of tropical Leguminosae had previously been studied by others—we may mention in particular the admirable investigations of Charles and Francis Darwin—but a definite explanation of their biological significance has only been arrived at through the most recent researches, carried out in the tropics and under the natural conditions of life of the plants. A visit to the botanical station at Buitenzorg, in Java, enabled Stahl and Haberlandt to shed some new light on the subject, and to show that the closing and erecting of the feather-like leaves of these plants is essentially connected with a proportionate diminution of the force of the tropical showers of rain, as well as with the regulation of the amount of light that falls upon them; for the more they are exposed to the sun the more do they become directed upwards, until eventually they close completely. This is at any rate the case in numerous other tropical Leguminosae, in which it is not the impulse of touch which starts the movement, but a certain intensity of the light:—the closing of the leaves here serves as a protection not only from the rain, but also from the excessive effects of the sun's rays. The leaves of these plants close when the light is strong, as well as when it is not so, and in the latter case the adaptation is looked upon by Haberlandt as an arrangement which causes the closing of the leaves even before the rain begins, when the sky is usually considerably clouded over. Compare Stahl, 'Regenfall u. Blattgestalt.; ein

Beitrag zur Pflanzenbiologie.' *Extract du Jardin Botanique de Buitenzorg*, vol xi., 1893; and Haberlandt, *Eine botanische Tropenreise*, Leipzig, 1893, pp. 112 and 113.

NOTE II (p. 11).

The matter is, if possible, still clearer in the case of geotropism, for there is no doubt that the habit of the plant to react in some particular way to the force of gravity cannot be a general and primary peculiarity of plants. A Volvox colony, rotating freely in water, is in a sense a living klinostat, uninfluenced by the attraction of the earth. The geotropic sensitiveness of plants can only have arisen when they became attached to the ground, and may therefore, even in its most general form, be regarded as an adaptation. This becomes much more evident when we consider that the various parts of existing plants have totally different susceptibilities to the stimulus of gravity: not only may the root be positively geotropic, while the stem is negatively geotropic, but each of the secondary roots and of the branches passes off at a perfectly definite angle from the primary root and stem, and this angle is due, at least to a certain extent, to a reaction to the stimulus of gravity. Thus the geotropic sensitiveness of plants, just like the sensitiveness of their different parts to light, may manifest itself in opposite manners; and—what is still more noteworthy—the sensitiveness is specially regulated for every part in such a way that the plant is enabled to adapt itself most advantageously to its different conditions. But a mode of reaction which responds very differently to the same stimulus cannot be originally or primarily characteristic of the plant: it cannot always have been possessed by all plants, but is due to an adaptation in connexion with the fixed condition of these organisms. The delicate 'molecular' structure, to which this wonderful sensitiveness is to be referred, cannot depend upon the direct action of external stimuli, but only on their indirect influence, i. e. on processes of selection.

NOTE III (p. 13).

That the principle of intra-selection is at work in plants just as in animals is seen from other than merely general considerations. Vöchting has recently described some experiments with plants which were kept in a feeble light. These at first showed marked effects therefrom, producing, for instance, flowers that were much below the usual size; they afterwards, however, 'adapted' themselves to the abnormal illumination, and yielded flowers of the normal size. This adaptation is probably to be referred to intra-selection. (Compare Vöchting, 'Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen,' Berlin, 1893, p. 11.)

Moreover, all the various adaptations of the parts of plants to the special influences that affect them, such as gravity, light, moisture, and chemical stimuli, must likewise be referred to the process of intra-selection. The delicate sensitiveness of tissue and protoplasm is hereditary, but it is through the struggle of parts that special adaptation to the actual conditions is secured. To take one example, already quoted above: the form of a tree is adjusted to the gap between other trees—vigorous growth takes place on the side next the light, while the shoots are retarded on the shaded side.

NOTE IV (p. 14).

Wilhelm Roux, *Der Kampf der Theile im Organismus.* Leipzig, 1881.

In this important treatise the principal subject discussed in addition to that of the spongy substance of bones is the form and branching of the blood-vessels in vertebrates. It is shown that these are constructed on the most suitable mechanical principles. For example, the lumen of a blood-vessel, where it leaves a larger trunk, is not of the usual cylindrical form, but is conical, and thus has the form which a free jet from a round lateral opening in the trunk would

assume in virtue of the pressure of fluid from within. The form, moreover, varies according to the angle which the branch makes with the trunk and the relative sizes of the two vessels. There is consequently the smallest possible amount of friction of the blood on the walls of the vessels through which it circulates; and as the number of branches of the vessels is immense, we must acknowledge the importance of an arrangement which largely helps to render possible 'the working of the circulation with a minimum expenditure of vital energy and of the vascular tissue.'

NOTE V (p. 22).

See F. Merrifield, 'The Colouring of *Chrysophanus phlaeas* as affected by temperature,' *The Entomologist*, December, 1892, and December, 1893. The results arrived at by this accurate observer agree very well with those I obtained with regard to the same butterfly, a brief account of which is given in *The Germ-Plasm: A Theory of Heredity*. London, 1893, p. 399.

The fact that a *direct* action of the temperature is concerned in the case of *Polyommatus* (*Chrysophanus*) *phlaeas* and that the change of colour is not due to some special adaptation is shown by the observations of Fritze, who found the individuals of this species in South Japan were almost entirely black in the warmest part of the summer. Cf. Fritze, 'Ueber Saison-Dimorphismus und Polymorphismus bei japanischen Schmetterlingen.' *Berichte der naturf. Ges. zu Freiburg i. Br.*, Bd. VIII, 1894, pp. 152–162.

While referring to Merrifield's valuable researches perhaps I may be allowed to call attention to the inconvenience resulting from recording temperature in degrees of Fahrenheit's scale in such works. Physicists and chemists have long since agreed to make use of the Centigrade scale in their writings; and it would be a great gain to scientific men in all the non-English countries if the zoologists of England and America would also adopt this usage. It is troublesome

to have to convert degrees of Fahrenheit into Centigrade, and as a rule a remainder is left, so that one has constantly to work with fractions. Moreover no distinct picture is suggested to the mind of those unaccustomed to the use of Fahrenheit's scale.

NOTE VI (p. 24).

An observation of Dr. Adalbert Seitz, the well-known authority on butterflies, also seems to me to indicate that seasonal dimorphism, dependent on adaptation, may in fact occur. Dr. Seitz relates in his interesting 'Reiseskizzen' (*Stettiner entomologische Zeitung*, 1893, p. 27) that on the hills near Yokohama, in Japan, numerous butterflies are to be found flying about as late as November. Their 'lower surface is leaf-like, and this is the more noteworthy as the summer-generations of the same butterflies are different in this respect; the autumn-form of *Grapta C. aureum* has consequently been described as *G. pryeri*, and *Terias laeta* and *T. Jaegeri*, which are only different generations of a seasonally dimorphic butterfly, have long been regarded as distinct species.' The author explains the adaptation by referring to the fact that at that time of year even the last remnants of the green leaves have disappeared, while the ground is strewn with withered leaves. It would be interesting to follow out this incidental allusion more carefully. It would not only show how marked and constant the differences between the two generations are, but would also prove the biological value of these differences; for whenever dimorphism depends on processes of selection, each of the forms is an adaptation, and must have a biological significance. For instance, if the colouration of the underside of the summer-generation were of no importance—that is, if the pattern might equally well be leaf-like—it would be difficult to see why the adaptation of the autumn-generation to dried leaves should not have extended to the other generation as well. This consideration is also valid in the case of *Vanessa levana-prorsa*. We cannot hold the adaptive nature of this seasonal dimorphism

to be proved as long as no explanation is forthcoming of the biological value of the colouration in the spring form *V. levana.* After the above lecture had been delivered, I received a recent paper by Dr. Brandes ('Der Saison-Dimorphismus bei einheimischen u. exotischen Schmetterlingen'; Halle, 1894), in which it is shown that a series of tropical butterflies are probably seasonally dimorphic in a manner similar to that which I have supposed to occur in *Vanessa prorsa*, the difference between the two forms being due to the adaptation of one generation to certain seasonal surroundings. Although these cases are not conclusively proved, I do not doubt that a seasonal dimorphism depending on adaptation exists. We must therefore distinguish between two kinds of seasonal dimorphism:—that which is called forth by the direct influence of temperature acting on the germ-plasm and on the growing scales, as well as an *adaptive* seasonal dimorphism, due to adaptation of *both* generations to different external surroundings. In the first instance, the temperature is the actual cause of the change in colouration; while in the second case it only serves as the stimulus which decides whether one or the other of two kinds of colouration shall appear.

NOTE VII (p. 28).

Rotifers, as is well known, produce two kinds of eggs, large ones that give rise to females, and small ones from which males arise. According to Maupas ('Sur le déterminisme de la sexualité chez l'Hydatina senta'; *Compt. rend*, T. 113, pp. 388–390), the same female always brings forth the same kind of eggs—either male alone or female alone; and it can be proved that whether a mother will produce daughter-forms which will bring forth male eggs, or daughter-forms which will produce female eggs, depends on the higher or lower temperature of the water in which the mother lives. We can make the mother produce alternately male-producing daughters or female-producing daughters; so

that in this case the sex is determined before the egg, concerning which the decision is made, has come into existence. This remarkable and rare arrangement is beyond doubt connected in the first place with the peculiar smallness of the males, and with the dimorphism of the eggs which is conditioned by this. We may go the length of asking why those daughters which yield male eggs are produced when the temperature of the water is high, and why those which give rise to female eggs are produced when the temperature is low:—this could hardly be a chance effect of temperature, but is much more likely to be due to an adaptation to the peculiar conditions of life in these animals. Sexual reproduction seems often to take place late among the rotifers, when the colony has almost reached the height of its development; but this will usually coincide with the occurrence of the highest temperature, so that, by the arrangement referred to, it is secured that the males appear at the most suitable time. If this interpretation is the correct one, we may understand why it happens that in this case the determination of sex is dependent on temperature, and why the higher and lower temperature produce the effects described.

NOTE VIII (p. 28).

Watasé, in a paper which appeared in 1892, 'On the Phenomena of Sex-Differentiation' (*Journ. of Morphology*, vol. vi. Boston, 1892), attempted, in a manner not quite clear to me, to conceive of sexuality itself as a phenomenon dependent on stimulus. With such a view I cannot agree, as will appear more plainly further on in this lecture.

NOTE IX (p. 31).

The experiments with *Musca vomitoria*, here described in outline, were made in the years 1884 and 1885 and have not hitherto been published, as I intended to extend them in another direction.

NOTE X (p. 31).

The normally-fed fly larvae required just as much time for their development into the adult form as those that were poorly fed—namely 206 hours; and they fed almost continually during the whole time. The ill-fed larvae were only allowed to feed for 138–150 hours, i. e. six-tenths to seven-tenths of the normal time. But these figures express the difference in the feeding of the two lots very imperfectly: the difference was, in fact, much greater, as is evident from the fact that the ill-fed larvae grew much more slowly and remained much smaller than the others. We may therefore say that at any stage in the 138–150 hours of their larval life they were less capable of taking nourishment than they would have been had they been of normal size on reaching this stage.

NOTE XI (p. 35).

I formerly indicated, not without good reason, that the eggs break down to help in sustaining the animal: this is at any rate the result of their disintegration, though perhaps it is simply an unavoidable and not an intentional one. The flies already referred to furnished another proof as to the extent in which the maturation of egg-cells depends on food. I had begun my experiments by endeavouring to find out whether the flies would reproduce at all in confinement: this could not be predicted of them, for many insects — butterflies, for instance—in general do not do so. And, in fact, it seemed at first as if the same would be true in this case also; for, in spite of abundant feeding with carrots and sugar, more than a month passed without any eggs being produced. As soon, however, as I introduced some meat into the case containing flies, they all darted down upon it, and greedily sucked its juice. In their craving for flesh they crowded on to the piece; and the result was that in a week afterwards a great number of eggs were laid. The quantity of nitrogenous food had therefore been too small, and without it the eggs could

not come to maturity; for the ovaries of flies are fully formed though very small when the insects escape from the pupa. In later experiments, when the flies were fed from the first with sugar and meat-juice, the eggs developed very rapidly in the ovaries, and the first deposit occurred as early as ten days after metamorphosis

It therefore appears that however rich the food of the larvae of these flies may be, it is only sufficient to form the ovaries, and not to bring any part of the egg-cells to maturity; and this seems to be equally true of bees and ants. Rich food is necessary in the imago-stage if the egg-cells are to ripen; and this probably explains the fact that the worker bees and ants as a rule produce no eggs: for they have usually to work hard to provide themselves with food, while the queens are supplied with rich food even in the imago-stage. It does exceptionally happen that the workers take rich food and exhibit an increased metabolism; and then they too bring the germs in their few egg-tubes to maturity, and lay eggs. Possibly we may explain Wasmann's experiments in a similar manner. (Cf. E. Wasmann (S. J.), 'Parthenogenesis bei Ameisen durch künstliche Temperaturverhältnisse,' *Biol. Centralbl.* Bd. xi. No. 1, Febr. 1, 1891). He frequently observed the production of eggs by the worker ants of several species he examined when the temperature was artificially raised. Warmth increases and accelerates metabolism and consequently stimulates the appetite. Moreover the experiment affected different species in different degrees, and this can be explained by the supposition that the ovaries had degenerated in different degrees. When they contain no egg-tubes at all, as in the case of *Tetramorium caespitum*, even the richest nourishment is of no avail to cause the production of eggs.

NOTE XII (p. 39).

In my book on *The Germ-Plasm*, I have simply spoken of double or multiple *determinants* as the foundation of dimorphism or polymorphism in the idioplasm. I conceived

dimorphism to originate in such a way that the determinants of an id first became double, and subsequently the doubled determinants varied in different directions. Repeated consideration of the facts now leads me to hold the modified view of this text as more accúrate. I now suppose that constitutional dimorphism of a species—even sexual dimorphism—is due to homologous determinants varying differently in different ids: so that, for example, one id contains 'male' and another 'female' determinants of the reproductive organs, of the genital ducts, or of the pattern of wings, and so on. In like manner I imagine that every other kind of dimorphism or polymorphism has originated by the different variation of corresponding determinants of the various ids. *Seasonal* dimorphism alone, so far as it depends only on the direct effects of external influences, implies no difference in the ids of the germ-plasm. Compare *The Germ-Plasm*, pp. 379, 380.

My present view seems to have the advantage of simplicity, as it does not require the hypothesis of a doubling of the determinants involved prior to the different variations—a complication that, as I was quite aware, could not well be accounted for. It permits, too, a perfectly gradual increase of the differentiation of the ids until a complete distinction arises in all the determinants of the id, so that two or more essentially different kinds of id constitute the germ-plasm. Moreover even a complete separation of these into two groups is possible, and must actually occur among species with male and female eggs.

This view of the facts also affords a deeper insight into the causes of the determination of sex. For if there are special 'male' and 'female' ids, the number of them in certain circumstances will give the decision as to whether the developing organism shall be male or female. For though in some cases sex is probably or even certainly determined by external influences which affect the egg, these are not to be regarded as the only or even principal cause of the decision *in all* cases: we are here concerned with an adaptation to special circumstances. In the case of human beings it appears very obvious that in a certain sense sex may be

hereditary:—I mean that the determination of sex may be dependent on the composition of the germ. The fact that many families consist chiefly either of male or of female children could hardly be accounted for in connection with any external influences. If, however, we conceive of the germ-plasm as composed of 'male' and 'female' ids, the numerical relations of these will usually be as 1 : 1. But deviations in this respect will occur, and may be increased by means of the processes of 'reducing division' and 'amphimixis'; and when a certain point has been reached they may lead to all or the majority of the children of the same parents being of one sex. I hope to treat of this matter in greater detail on another occasion.

The idea that sexual dimorphism is based on the presence of more or less markedly different 'male' and 'female' ids in the idioplasm, harmonizes very well with the occasional determination of sex by external influences. Just as the 'worker-ids' of the bee become active by the poor food-supply of the larva, while the 'queen-ids' remain inactive, it would seem to be possible that in the case of the frog abundant nourishment in the larval stage should usually lead to 'female' ids becoming active, while meagre feeding leads to a preponderance of 'male' activity. In like manner it is possible that in the case of the bee any factor that is connected with the act of fertilization might be the means of stimulating the female-ids to activity.

NOTE XIII (p. 43).

I am quite aware that pathological abnormalities occur in which entire parts or organs may be wanting. But such cases do not contradict the view of the phyletic nature of the process by which typical parts become rudimentary, to which I have given expression on p. 35. It is true that the brain may be partly or altogether wanting in a human embryo or may be abnormally small, or defects may occur in the heart, or larger or smaller regions of the limbs may be wanting;

but such abnormalities are never due to a general insufficiency of nourishment. They may depend, as E. Ziegler shows (*Lehrbuch der path. Anat.* 1892, p. 369), either on the transmission of abnormal primary constituents of the germ, on primary pathological variations of the germ, or on external injuries: thus, for instance, a constriction of the limbs of the embryo by the umbilical cord or the egg membranes may occur.

NOTE XIV (p. 43).

Until lately it had only been demonstrated in the case of bees that food differences determined whether the female larvae should become workers or queens. The quality and quantity of the food which the different kinds of bee-larvae receive is accurately known, chiefly owing to the beautiful researches of Planta. In the case of ants there is a lack of evidence; but very valuable and definite information has recently been obtained on this point as regards termites, concerning which we were previously very ignorant. Grassi and Sandias's observations in Catania ('Costituzione e sviluppo della Società dei Termitidi. Osservazione sui loro costumi etc.'; Catania 1893, *Atti dell' Acad. Gioenia di Sc. nat.* Vol. VI *e*, VII) have shown that, in the Sicilian termites, the egg, like that of the bee, contains the primary constituents of each kind of individual. Whether the development of the male is determined by the absence of fertilization must still be left an open question; but it has been definitely established that the larvae of the fertile females receive far more abundant and more nourishing food than do the young which will give rise to workers or soldiers. Moreover, even at a later stage, the larvae can at will be reared either as fertile forms or as barren workers or soldiers; and here again it is a nutritious secretion of the insect itself which leads to the production of the sexual form. Just as in the case of bees, the larvae for three days are all fed with this nutritive secretion, after which time only those which are destined to become sexual forms continue to receive it regularly, the

others getting it not at all or only in small quantities. The sensitiveness of the larva to differences in nutrition must, however, be more finely graduated in termites than in bees; for Grassi has shown that even the distinction between workers and soldiers is under the control of the food providers. If the soldiers are taken away from them, they make new ones from other larvae.

NOTE XV (p. 44).

Herbert Spencer has attempted to weaken my reference to the social insects as an illustration of the metamorphosis of an organism taking place apart from any transmission of acquired characters (Cf. Weismann, 'The All-Sufficiency of Natural Selection; a Reply to Herbert Spencer,' *Contemp. Rev.*, Sept. and Oct., 1893), by maintaining that the characters of the neuters had originated while all the females were still prolific. I will not deny the possibility of some of the peculiarities of the workers having actually originated as far back as this, though it would be difficult or even impossible to be at all certain on this point. But it seems to me that there is no room for doubt that the greater part of the characteristics of the workers have arisen later—that is, during and after the formation of castes. Herbert Spencer looks upon the infertility as a direct consequence of inadequate nourishment of the larvae. I have just shown that this cannot be so; but if, for a moment, we assume the contrary, how could we account for the instinct of the workers at the present day, which leads them to take far less food than the fertile females when in the imago-stage? Surely this cannot be explained by the meagreness of the nourishment during the larval stage! In my experiments with flies, at any rate, those which were poorly fed showed no less appetite as *imagines* than their sisters which had been well fed as larvae. Or ought we to suppose that the habit dates from ancient times, when all the females instinctively took but little food? In this case they would

not have reproduced, as the workers at the present day cannot mature the scanty egg-cells present in their few egg-tubes. And we must not forget the double, or—in the case of some ants and the termites—three-fold forms of the workers, to which I referred in this connection in my essay! But I may spare myself further reply to the completely untenable contentions of Mr. Spencer, for Mr. Platt Ball has already admirably answered him in a paper on 'Neuter Insects and Lamarckism' (*Nat. Science*, vol. iv., Febr., 1894). One of the questions put to Spencer by Ball is quite sufficient to show the utter weakness of the position of Lamarckism:—if their characteristics did not arise among the workers themselves, but were transmitted from the pre-social time, how does it happen that the queens and drones of every generation can give anew to the workers the characteristics which they themselves have long ago lost?

That I am not alone in regarding the case of the neuters of ants and termites as affording a proof against the theory of the inheritance of acquired characters is also seen by reference to Prof. Lloyd Morgan's book on 'Animal Life and Intelligence' (London, 1890–91). Although this author is still doubtful whether we are right in not acknowledging the Lamarckian principle, he also cites the case of the soldiers of certain ants (*Oedocoma cephalotes*) possessing enormous heads and mandibles as furnishing an argument against the views of Herbert Spencer. 'The possession of these parts so inordinately developed must necessitate many correlated changes. But these cannot be due to inherited use, since such soldiers are sterile' (loc. cit., p. 213). A good dialectic combatant might certainly maintain in opposition to this argument that this supposed sterility is not proved:—although soldier-ants in all known cases have been found to be sterile, it is known that ordinary workers often lay single eggs; and this may not be an exception,—as is assumed by the opponents of the Lamarckian principle,—but may, in fact, be the rule. Such unfertilized eggs produced by the workers may be destined to give rise to the *males* of the colony, and thus the changes acquired